Eubalichthys gunnii (Gunther)	Gunn's Leatherjacket
Eubalichrhys mosaicus (Quoy & Gaimard)	Pigmy Leatherjacket
Brachaluteres jacksonianus (Quoy & Gaimard)	Pigmy Leatherjacket
Scobinichthys granulatus (Shaw)	Rough Leatherjacket
Acanthaluteres spilomelanurus (Quoy & Gaimard)	Bridled Leatherjacket

Pollination and Fruit Production of *Cupaniopsis anacardioides* (A. Rich.) Radlkf. (SAPINDACEAE) at Townsville, North Queensland. 1. Pollination and Floral Biology.

By T. J. Hawkeswood*

Abstract

Observations on insect pollination vectors of *Cupaniopsis anacardioides* (A. Rich.) Radlkf. (Sapindaceae) were made on the 7 August, 1981 on the James Cook University grounds, Townsville, north Queensland (c. 19°15'S, 146°48'E). Six insect species were collected from the flowers and their pollen loads examined and compared. Only two insect species, *Stomorhina discolor* (Fabricius) (Diptera: Calliphoridae) and *Trigona carbonaria* Smith (Hymenoptera: Apidae) were common visitors. The most efficient pollinator is considered to be *T. carbonaria*. The flowers of *C. anacardioides* possess more features of cantharophily and myophily than melittophily, yet are mainly pollinated by small bees (i.e. *Trigona*) at Townsville. Further observations on pollination vectors throughout the plant's range and embryological studies are needed.

Introduction

Cupaniopsis anacardioides (A. Rich.) Radlkf. is a medium-sized, slender, mostly glabrous, tall shrub to tree, usually attaining a height of 3-5 metres, with compound leaves, belonging to the Sapindaceae.

According to Bentham (1863), *Cupaniopsis* (as *Cupania*), is a tropical genus of trees with all the Australian species being endemics. Oakman (1964) notes that *C. anacardioides* is indigenous to the east coast of Australia where it may be found growing in isolated clumps or as single specimens. According to Oakman (1964), although the species flourishes on the sandy coastal strips and its roots "reach a considerable distance to the water table", *C. anacardioides* is not affected by average winds and can withstand heavy salt sprays. It is thus a hardy tree and is particularly suitable for streets with considerable wind exposure in association with poor soil conditions (Oakman, 1964, p. 183).

The genus name (originally *Cupania* for the species) is derived from the Italian botanist, Francesci Cupani, and the specific epithet refers to the fruits which apparently resemble the cashew nut (*Anacardium*, Anacardiaceae) in general appearance (Oakman, 1964).

Despite this species being well-known in cultivation, little is known about its natural past or present distribution in eastern Australia, pollination ecology, fruit and seed production, and seed viability. Specimens of *C. anacardioides* which have been planted on the James Cook University campus, flowered during early to mid-July 1981 and thus provided an opportunity for subsequent study of some of these aspects.

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Materials and methods

(a) Collection of insect pollination vectors and pollen examination.

Insects were randomly collected, using a hand net, from the open flowers of one tree of *C. anacardioides* (the most profuse flowering specimen) on 7 July 1981, between 1300-1350 hrs (EST). After capture, the specimens were carefully transferred from the net and deposited in a large glass killing jar containing a cotton wool pad sprinkled with ethyl acetate (as per Hawkeswood, 1981). The insects were then examined for pollen loads at James Cook University, Townsville, with the aid of a high-power dissecting microscope. Pollen grains were usually clearly visible as small to large clusters or individual grains, adhering to hairs or more usually to the general body surface of individual insects. Pollen grains from five bees (*Trigona carbonaria* Smith) and three flies (*Stomorhina discolor* (Fabricius)) were examined and compared under a 100X-1000X binocular microscope with grains from fresh, open flowers of *C. anacardioides*. The pollen grains from these insects were identical to those from the flowers, indicating that the insects were transporting pollen grains of *C. anacardioides*.

A list of the pollination vectors and data showing places of pollen deposition are provided in Table 1. Voucher collections of the fly species (Diptera) examined are deposited in the Australian National Insect Collection (ANIC) in Canberra, while voucher collections of the bees and wasps are deposited in the University of Queensland Insect Collection (UQ) in Brisbane. Voucher colleetions of *Cupaniopsis anacardioides* are deposited in the Queensland Herbarium (BRI) in Brisbane.

(b) Study site

Two plants from a group of 12 *C. anacardioides* trees (about 2.3-3.5 m high), planted in a row alongside a walkway in the centre of the James Cook University grounds, were examined in this study. On 9 July 1981, during flowering (flowering commenced on about 5 July and ceased on about 26 July 1981), samples of flowering branches were taken (using a long-handled pruner) from two trees (the most profusely flowering specimens). This procedure was undertaken in order to examine the number of open flowers and the number of flowers/inflorescence to gain a rough estimate of the number of flowers produced per tree (Table 2).

Other dicotyledonous plants which were also flowering on the University grounds at the time include species of *Thunbergia* (Acanthaceae), *Tridax* (Asteraeeae), *Stenolobium* (Bignoniaceae), *Bauhinia* and *Caesalpinia* (Caesalpiniaeeae), *Calliandra* (Mimosaceae), and *Antignon* (Polygonaceae). These were briefly examined for insect vectors in order to ascertain whether the insect species visiting *C. anacardiodes* also visited these other plants.

Results

(a) Pollen grains

The pollen grains of *Cupaniopsis anacardioides* (Fig. 1) are small, solitary, sub-triangular in shape, 3-porate (with three pores), 3-colpate (with three furrows), syncolpate (furrows of uniform width, orientated meridionally and fused at the poles) and have a distinctive sexine pattern (Fig. 1). The grains have an equitorial diameter of 8-10 μm and a polar axis of 6-8 μm.

(b) Pollination vectors

A total of 6 insect species (3 flies and 3 bees) were collected from the flowers (Table 1). Only two of these, i.e. *Stomorhina discolor* (Fabricius) (Calliphoridae) and *Trigona carbonaria* Smith (Apidae) were common (Table 1). On the other hand, *Dacus murrayi* (Perkins) (Tephritidae), *Baccha* sp. (Syrphidae), *Apis mellifera* Linnaeus (Apidae) and *Palaeorhiza* sp.

(Colletidae) were uncommon and an estimate of the numbers present for these species was not undertaken (Table 1).

The most important pollinator appears to be the workers of the small, black, native bee species, *Trigona carbonaria* Smith (body length 0.4-0.5 cm). All 12 specimens examined carried *Cupaniopsis* pollen, mostly on the abdomen and legs (Table 1); 8 specimens (66.6% of the total examined) carried large pollen bags on both the hind legs (Table 1). One bag from each of two bees was squashed under a coverslip on a microscope slide and examined with a compound microscope. Examinations showed that the bags comprised 100% of *Cupaniopsis* pollen, indicating that the bees were specific on *Cupaniopsis* flowers during the flowering of the species.

Specimens of *Trigona carbonaria* spent on the average 5-20 seconds feeding from individual flowers of *Cupaniopsis* before either (a) visiting 1 or 2 more flowers on the same inflorescence, (b) flying to another inflorescence on the same tree, (c) flying away to another tree nearby, or (d) flying away from the study area. Individual worker bees almost invariably contacted anthers and stigmas during flower visitation and pollen collection. The observations on *T. carbonaria* suggest that the species effects a high level of self-pollination (geitonogamy) of *C. anacardioides* at Townsville, and a low level of cross-pollination (xenogamy).

The calliphorid fly, *Stomorhina discolor* (Fabricius) (body length 0.55-0.7 cm) was common (Table 1) but only small amounts of pollen (usually less than 20 grains per fly) were found on their bodies (usually on the abdomen and legs, Table 1). The flies spent most of the time hovering in the air within one metre from the crowns of the trees or flying around the tops of the trees before rapidly darting into an in-

Table 1. Pollinators of Cupaniopsis anacardioides (A. Rich) Radlkf. on the James Cook University grounds, Townsville, north Queensland. (Places of pollen deposition on insects are shown by asterisks. Underline marks show where the majority of pollen was placed on the majority of specimens examined. Format follows that of Nilsson (1978) and Hawkeswood (1981)).

Species	Number of specimens collected	Estimated number present	Place of pollen deposition: Antennae	Head	Eyes	Thorax	Abdomen	Legs	Wings
DIPTERA									
Calliphoridae									
1. Stomorhina discolor (Fabricius)	15	c.100*	–	+	+	+	±	±	+
Tephritidae									
2. Dacus murrayi (Perkins)	3	c. 2 ?	–	+	–	+	+	±	–
Syrphidae									
3. Eristalis sp.	1	unknown	–	+	+	+	+	+	±
HYMENOPTERA									
Apidae									
4. Trigona (Tetragona) carbonaria Smith	12	200*	+	+	+	+	±	±	+
5. Apis mellifera Linnaeus	2	unknown	+	+	+	+	±	±	+
Colletidae									
6. Palaeorhiza sp.	1	unknown	–	–	+	+	±	+	–

florescence to feed on pollen (usually from only one flower), and then darting out again. They spent short periods of time feeding (5-15 seconds in most cases). When feeding, they often fed from outside the flower and not on the flower (i.e. stamens, petals and sepals) as did *T. carbonaria*. Some individuals of *S. discolor* were also observed to spend some time resting on leaves grooming the head, antennae and legs (tibiae). This behaviour may explain the absence of pollen on the antennae in 15 specimens examined (Table 1), while only 1-5 grains were detected on the head and eyes. The role of this fly in the pollination of *C. anacardioides* at Townsville is probably much less than that of *Trigona carbonaria* which carries larger pollen loads and is small enough to feed within the *Cupaniopsis* flower amongst anthers and stigmas thereby effecting pollination.

Due to their small numbers and amount of pollen carried on their bodies (often less than 20 grains per insect were detected), the native species of *Dacus murrayi* (Perkins) (body length 0.7-0.9 cm), *Baccha* sp. (body length 1.0-1.2 cm) and the green bee *Palaeorhiza* sp. (body length 1.3-1.5 cm), probably play a minor role in *C. anacardioides* pollination at Townsville. The majority of grains were carried on the legs of *Dacus murrayi,* on the wings of one specimen of *Baccha* sp. (the other specimen did not carry any pollen), and on the underside of the abdomen of *Palaeorhiza* sp. (see Table 1).

Pollen of *C. anacardioides* was detected on all parts of the body on the two specimens of *Apis mellifera* Linnaeus examined, but mostly on the abdomen and legs (Table 1). The feral bees are probably efficient pollinators of *C. anacardioides*, but due to their low numbers visiting flowers at the time of observations, they may not be as impor-

TABLE 2. Quantitative data on some flowering characteristics of two trees of Cupaniopsis anacardioides (A. Rich.) Radlkf. at Townsville, on 9 and 12 July, 1981.

Date	Tree	Inflorescence Sample No.	Number of open flowers	Number of * flowers per inflorescence	Percentage (%) flowers open	Number of racemes per inflorescence
9 July	1	1	10	263	3.8	3
	1	2	42	362	11.6	6
	1	3	48	215	22.3	11
12 July	1	1	9	290	3.1	5
	1	2	21	204	10.3	4
	1	3	42	298	14.3	5
	2	1	26	255	10.2	5
	2	2	0	332	0.0	9
Totals	-	8	198	2219	-	48
Mean and standard deviation	-	-	24.8±17.9	277.4±54.4	9.45±7.13†	6.0±2.7
Range	-	-	0-48	204-362	0-22.3	4-11

* Inflorescence = One terminal (or axillary) panicle of racemes.

† These figures are the mean and standard deviation of the percentages. The average (mean) of the total number of open flowers/total number of flowers per inflorescence counted (i.e. 198/2219) is 0.0892 or 8.92%.

Fig. 1. Scanning electron micrograph of a fertile pollen grain of *C. anacardioides*, showing the tricolpate nature of the grain and the reticulate pattern of the sexine wall. Bar indicates 5 m (1 μm = 10^{-6} m).

tant as the native bees *Trigona carbonaria*.

(e) Observations on the flower

The actinomorphic (regular), usually bisexual flowers are small, (7-9 mm in diameter when fully open), (although according to Bentham (1863) they are large for the genus), and are arranged in long, axillary or terminal panicles of racemes, 18-35 cm long. Each flower has five, free sepals which are imbricate in bud. These sepals are orbicular in shape, with slightly ciliate margins; three are larger (c. 4.5 mm long, 3.0 mm wide) than the other two (c. 2.5 mm long, 2.5 mm wide). The petals are small, deltoid in shape, 1.5-1.8 mm long, acute, with two, very short, obovate, hirsute scales at the base. There are usually 8-10 stamens per flower, inserted between the ovary and the hypogynous disc surrounding the ovary. The anther filaments are short, c. 1.3-1.4 mm long, hirsute at the base, while the anthers are oblong, 1.8-2.1 mm long, and dehisce longitudinally. The ovary is hypogynous and villous with a short, simple style.

Flowers open in the early morning (c. 0700-0830 hrs, EST) and during the morning begin to emit a strong, distinctive, fragrant odour which persists into the afternoon. This period of scent production appears to correspond with the period when the insect visitors are most active. The flowers exhibit only slight protandry; the anthers dehisce immediately before or at about the time of anthesis (as indicated by dissecting closed and almost opened flowers). If the flowers are not pollinated by the early to mid afternoon, they fall from the plant during the late afternoon. Pollen, which is produced in large quantities per flower, appears to be the main attractant to the insect vectors, while the sweet-scented nectar produced from the very large hypogynous glands, may act as a secondary attractant luring the insects to the flowers.

The flowers appear to be functionally

bisexual, although the Sapindaceae are well-known for their polygamous flowers (i.e. the inflorescences have bisexual and unisexual flowers mixed together). Examination of numerous randomly selected flowers from different trees indicated that normally shaped, fertile pollen grains were produced by all flowers. All flowers had well-developed hypogynous glands and apparently a functional ovary and stigma. It is likely that the majority of *C. anacardioides* flowers are bisexual but a low percentage (i.e. $\leqslant 5\%$) are in fact, unisexual. This aspect of *Cupaniopsis* floral biology was not investigated in detail due to insufficient time.

In a sample of 8 inflorescences collected on 9 and 12 July 1981, at about 1550-1630 hrs (EST) between 0 and 48 flowers had opened during the day per inflorescence (Table 2) and were still persistant on the rhachis. The percentage of flowers open per inflorescence in the samples examined varied between 0.0% and 22.3% (Table 2), with an average of 9.45 ± 7.13% (Table 2). Considering an average of about 280 flowers per inflorescence (Table 2), then between 0% and 17% of the total number of flowers per inflorescence (or tree) are open per day. On average, the number of open flowers per inflorescence is 24.8 ± 17.9 (Table 2) and the number of flowers per inflorescence vary from 204-362 (Table 2) with an average of 277 ± 56.4 (Table 2). I have estimated that between 100-250 inflorescences were produced by the trees growing on the James Cook University grounds at Townsville. Using the average of 277 flowers/inflorescence, then *C. anacardioides* trees may produce between 27,000 and 69,000 flowers during the flowering season, although 25,000-35,000 flowers per plant (mature tree) may be a more conservative estimate since not all the trees produce as many as 250 inflorescences. *C. anacardioides* is indeed a mass-flowerer.

Discussion

(A) *Cupaniopsis* and the syndromes of pollination

The flowers of *C. anacardioides* are (a) actinomorphic, (b) have few visual attractions, (c) are shallow, bowl-shaped, (d) cream to greenish in colour, and (e) possess a strong, fragrant odour. The attractants for insects appear to be the pollen (which is produced in large quantities) and nectar. The anthers and stigmas are exposed i.e. positioned above the level of the sepals and petals, while the ovary is hypogynous with a prominent gland which secretes the nectar.

Faegri and Van der Pijl (1976) have outlined various pollination syndromes e.g. pollination by flies is known as myophily, by beetles, cantharophily, and bees, melittophily. According to these authors, flowers possessing the syndrome of melittophily have all or most of the following features: (a) zygomorphic flowers, (b) strong flowers capable of supporting the weight of bees, (c) yellow or blue flowers, (d) nectar guides present; nectar hidden but not very deep, produced in moderate quantities, (d) odour fresh but not strong, (e) stamens and stigmas hidden inside the blossom, and (f) hypogynous flowers. *C. anacardioides* possesses only one of these features, i.e. hypogynous flowers. Based on Faegri and Van der Pijl's criteria, the flowers do not appear to be adapted for melittophilly.

Plants with the syndrome of myophily (small fly blossoms) have (a) actinomorphic flowers, (b) simple and shallow flowers without impression of depth, (c) light, dull coloured flowers, (d) nectar guides usually present, (e) imperceptible odour, (f) anthers and stigmas well exposed, and (g) an epigynous or hypogynous ovary. *C. anacardioides* possesses most of these floral characters but has a strong, pungent odour and lacks nectar guides.

Plants which possess the syndrome of

cantharophily have all or most of the following features: (a) flowers with no special or definite shape, and few visual attractions; they are generally flat, cylindric, or shallow, bowl-shaped and easy of access, (b) flowers which are dull, greenish or cream and have easily accessible attractants such as nectar and pollen, (c) flowers with a strong, fruity or aminoid odour, (d) anthers and stigmas exposed, and (e) an epigynous ovary. *C. anacardioides* possesses all these features except an epigynous ovary.

C. anacardioides flowers appear to be adapted for cantharophily according to Faegri and Van der Pijl's criteria. However, a majority of the flowers usually hang downwards or are positioned perpendicular to the vertically hanging rhachises of the inflorescence, and are probably not suited for beetles which usually require an upright, flat flower upon which to land and feed. In addition, most Australian anthophilous beetles are present as adults between early summer and early autumn and very few, if any, are present during July and August when *C. anacardioides* flowers (this is especially so at Townsville, T. J. H. pers. obs.).

Only extensive field work through the range of *C. anacardioides* will show whether small, anthophilous beetles, e.g. Mordellidae, do pollinate the flowers or whether bees and flies are the dominant vectors throughout its distribution.

(B) Insects as pollinators

(a) *Trigona carbonaria* Smith (Apidae)

Michener (1961) presented data on the nest architecture of certain stingless bees of the genus *Trigona*, and noted that *T. carbonaria* Smith was very common in coastal Queensland and extended as far south as Sydney, N.S.W. Michener found the species common and widespread in areas around Brisbane and also collected it from Bundaberg, Gladstone and Mackay, usually at the edges of rainforest but occasionally in *Eucalyptus* savannah woodlands. Rayment (1932a) recorded the possibility of pollen grains of *Eucalyptus* (Myrtaceae) and *Hardenbergia* (Fabaceae) being food for the larvae of *T. carbonaria*, and also noted (Rayment, 1932b) stored pollen of the following native genera in nests of the species — *Eucalyptus*, *Angophora* (Myrtaceae), *Hardenbergia* (Fabaceae), *Cassia* (Caesalpiniaceae) and *Xanthorrhoea* (Xanthorrhoeaceae). However, he did not examine pollen loads of the adults nor emphasize their importance in pollination in these papers.

Michener (1965, pp. 243-244) collected *T. carbonaria* from a wide range of host plants but did not provide any information on the species pollination ecology. He records the following plants visited for pollen and/or nectar from southern Queensland and north-eastern N.S.W. — *Eucalyptus tessellaris*, *E. tereticornis*, *E. intermedia*, *Angophora subvelutina*, *A. woodsiana*, *A. intermedia*, *Leptospermum microcarpum*, *L. flavescens*, *Callistemon salignus*, *C. viminalis*, *Melaleuca sieberi*, *M. bracteata*, *M. linariifolia* (all Myrtaceae), *Persoonia virgata*, *Banksia* sp. (Proteaceae), *Pultenaea villosa*, *Daviesia squarrosa*, *Jacksonia scoparia*, *Oxylobium ilicifolium* (Fabaceae), *Hibbertia linearis* (Dilleniaceae) and other miscellaneous plants. *T. carbonaria* has not been recorded previously from *Cupaniopsis anacardioides*.

Trigona carbonaria appears to be an important pollinator of *C. anacardioides* at Townsville. Being only slightly smaller than the flower (body length of the bee 0.4-0.5 cm; flower width 0.6-0.7 cm when open), the bees when foraging, are able to turn and move about the flower while feeding on nectar and gathering pollen. Since they carry a majority of their pollen loads on

their abdomen (Table 1) they are likely to frequently contact and brush pollen onto the stigma during each visitation.

(b) *Palaeorhiza* sp. (Colletidae)

Little is known of the biology of *Palaeorhiza*. Michener (1965) states the genus is centred in Papua New Guinea and individuals are common in areas covered by tropical rainforest. The Australian species of *Palaeorhiza* are badly in need of revision. Rayment (1935) recorded *Eucalyptus* as a food plant for *Palaeorhiza*. The genus, as far as the author is aware, has not been recorded previously from *Cupaniopsis* flowers. Due to their rarity on *C. anacardioides* flowers at Townsville, they are unlikely to play a major role in pollination of this plant in this area. Observations in other areas (e.g. Cape York Peninsula, where the bees may be more common) may show *Palaeorhiza* species to be important pollinators of *Cupaniopsis* and other plants.

(c) *Stomorhina discolor* (Fabricius) (Calliphoridae)

Dear (1977, p. 794) in an excellent review on the Australian Rhiniinae (Calliphoridae) noted that *S. discolor* (Fabricius) has a wide distribution in the Oriental, Austro-Oriental, Australasian and Pacific regions. In Australia it has been recorded from all States except Tasmania and is most common in Queensland and N.S.W. Dear (1977) notes that adults are on the wing throughout the year but are more common during March, April, November and December. At Townsville, the species has been observed to have an association with termites (Isoptera); adults have been bred from *Mastotermes* nests (Dear, 1977). The present paper is the first to record this fly as a pollinator. They appear to be mainly pollen feeders but will also sip nectar. It is likely that *S. discolor* visits a wide range of flowering plants for food throughout its distribution. Further observations will greatly add to our ecological knowledge of this fly.

(d) *Dacus murrayi* (Perkins) (Tephritidae)

The Tephritidae are commonly known as fruit flies because the larvae are fruit-eating. Their role in pollination has not been investigated in Australia. Although not an important pollinator at Townsville, *D. murrayi* (Perkins) may be more imporant in *C. anacardioides* pollination in other areas where they are more common.

(e) *Baccha* sp. (Syrphidae)

The Syrphidae are a common, widespread family of flies, many species of which are known to be pollinators (e.g. Proctor and Yeo, 1973). *Baccha* has not been previously recorded as a pollinator in Australia. Hardy (1933) recorded two species of *Baccha* (i.e. *B. monobia* Terry and *B. siphanticida* Terry) from Australia, but the genus is badly in need of revision. Further observations and collections of these flies should lead to a better understanding of their ecology.

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